A DESCRIPTION OF HORNED-TURTLE REMAINS (TESTUDINES:MEIOLANIIDAE) FROM THE MID-MIOCENE CAMFIELD BEDS OF NORTHERN AUSTRALIA

D. MEGIRIAN

Northern Territory Museum of Arts and Sciences, GPO Box 4646, Darwin, NT 0801, Australia

ABSTRACT

New horned-turtle fossil material from the mid- to late-Miocene Bullock Creek Local Fauna (Camfield Beds) of the Northern Territory of Australia is referrable to the genus *Meiolania* on the basis of its morphological similarity to the Pleistocene-aged *Meiolania platyceps* Owen from Lord Howe Island. A single individual is represented by cranial fragments, and second and fifth cervical vertebrae. In some details, the Bullock Creek *Meiolania* more closely resembles fragmentary material from New Caledonia, some of which has been assigned to a poorly defined taxon, *M. mackayi* Anderson. A species determination for the Bullock Creek *Meiolania* is not yet possible. The possible relationships of the New Caledonian and other undetermined Australian mid-Tertiary meiolaniids to *M. platyceps* are briefly discussed.

KEYWORDS: Horned turtle, fossil, Miocene, Camfield Beds, Australia, Meiolania.

INTRODUCTION

The Meiolaniidae are a most unusual, extinct family of large turtles from the Cainozoic of South America, Australia and several western Pacific islands. Meiolaniid skulls are elaborated by horns, frills and bosses, the cervical vertebrae bear ribs, and the tail is sheathed distally by a club. Owen's (1881) description of meiolaniid remains, mistakenly referred by him to the giant Pleistocene varanid, Megalania Owen, marked the beginning of more than a century of scientific publications on the group. Late nineteenth century confusion about the place of meiolaniids within the Reptilia and the subsequent controversy over whether they belonged with the cryptodiran or the pluerodiran turtles has been well recounted by Gaffney (1983) and this work is an excellent introduction to the earlier literature. On the basis of shared, derived skull characters, Gaffney (1975) places the Meiolaniidae with the Cryptodira. Further discussion of the phylogeny of the group at higher taxonomic levels is included in Gaffney (1983,1985).

In 1985 and 1986 members of the Northern Territory Museum's palaeontological expe-

ditions to Camfield Station collected fragmentary remains of a meiolaniid from the mid- to late-Miocene Camfield Beds. Meiolaniid fossils have previously been reported from the mid-Tertiary of Australia (Etheridge 1889; Gaffney 1981) so their presence in the Camfield Beds was not entirely unexpected. The Bullock Creek meiolaniid shows a general morphological similarity to the Pleistocene Meiolania platyceps Owen (1886) from Lord Howe Island, although in some details it more closely resembles fragmentary material, also Pleistocene-aged or younger, from New Caledonia described by Anderson (1925) and Gaffney et al. (1984). Some New Caledonian material-was assigned to a poorly defined species, Meiolania mackavi Anderson (1925), a taxon close to M. platyceps. The Bullock Creek form is referrable to the genus Meiolania, but a species determination is not yet possible. A description of the new material may be useful in future taxonomic studies.

The only other Australasian taxon, "Meiolania" oweni (Woodward, 1888) from the Pleistocene of Queensland and New South Wales, is clearly more closely related to the



Fig. 1. Bullock Creck *Meiolania* right squamosal fragment NTM P87103-2 in dorsal view. Posterior is towards the top of the page.

two Argentinian forms, Niolamia argentina Ameghino, 1899 from the pre-Oligocene, and Crossochelys corniger Simpson, 1937 from the Eocene. A reappraisal of this lineage, with its confusing literature (see Gaffney 1983:393), is in preparation by Gaffney. Useful descriptive references for these taxa are; Owen (1881) for "Meiolania" oweni, Woodward (1901) for Niolamia argentina, and Simpson (1938) for Crossochelys corni-Simpson (1938) also provides useful ger. comparisons, revised in some details by Gaffney (1983). Gaffney (1981) reviewed the then known Australian/Pacific island meiolaniid fossils, including undetermined material, and summarised principal differences between all the known forms.

Comparisons presented here are with published descriptions. Prefixes to catalogue numbers are as follows : AM Australian Museum, Sydney; MM Mining and Geological Museum, Sydney; NCP, NCT Muséum National d'Histoire Naturelle, Paris; NTM Northern Territory Museum, Darwin.

STRATIGRAPHIC PALAEONTOLOGY

The Bullock Creek Meiolania was recovered from the Camfield Beds at a location described by Plane and Gatehouse (1968) as "16 miles southeast of Camfield Homestead in the north central Northern Territory" (approximate latitude 17°S, longitude 131°30'E). The Camfield Beds are fluvial and lacustrine calcareous conglomerates, sandstones and siltstones, with basal ferruginisation and silicification on top. No suitable techniques are yet avaliable to establish the absolute age of the Camfield Beds, but on the basis of the stage-of-evolution of marsupial components of the Bullock Creek Local Fauna, a mid- to late-Miocene age is estimated. Woodburne et al. (1985) provide the most recent review of the biochronology of

Australian Tertiary vertebrate-fossil deposits and outline the methodologies used for estimating their ages.

SYSTEMATICS

Material. All the specimens listed below were collected from within a few metres of each other at a locality known informally as the "Blast Site". Their juxtaposition, preservation and respective sizes suggest that a single individual is represented. The fossils were extracted from their limestone matrix using acetic acid. Carapace and plastron fragments, and a dermal ossicle, were also recovered, but are not described here. They do not appear to differ in any noteworthy respect from *M. platyceps*.

NTM P87103-2, right squamosal fragment bearing a cow-like horn: NTM P87103-3, left squamosal fragment with the horn sheared off, but part of the cavum tympani preserved; NTM P8695-93, second cervical (axis) vertebra lacking right parapophysis; NTM P87103-4, fifth cervical vertebra lacking right parapophysis.

Description. Gaffney (1983) provides a detailed description of the cranial morphology of M. platyceps, and his terminology for cranial scale (scute) areas and the osseous excrescences encompassed by them is followed here.



Fig. 2. Bullock Creek *Meiolania* left squamosal fragment NTM P87103-3 in (a) left lateral and (b) internal views. The designation of epidermal scute areas (B, C and K) follows the system of Gaffney (1983).

NTM P87103-2 (Fig. 1) and NTM P87103-3 (Fig. 2) are composed wholly of right and left squamosal respectively; no osseous sutures are discernable on either fragment. The cavum tympani, partially preserved with NTM P87103-3 (Fig. 2), shows a close correspondence to the examples of *M. platyceps* (AM F16866) and *M. mackayi* illustrated in Anderson (1925, Plate 32, Figs 4 and 6 respectively).

On both Bullock Creek cranial fragments the B scute margins are clearly defined by shallow sulei, but others are less certain, partly because of their short truncation by the broken edges of the fragments. The interpreted scute patterns (Fig. 2 and Fig. 3) do not appear to differ from *M. platyceps*. In *M. platyceps*, perhaps uniquely within the Testudines, cpidermal sutures are marked on the skull by low ridges (Anderson 1925; Gaffney 1983).

The cowlike B horn core preserved with NTM P87103-2 projects from the posterolateral skull margin. Its angle of projection, when vicwed from the lateral or medial sides, is towards the posterior with little dorsal rise. The horn core is long, slender and terminates acutely. In any profile it is smoothly curved.



Fig. 3. Bullock Creek *Meiolania* horn-bearing cranial fragment, NTM P87103-2: (a) dorsal view; (b) ventral view; (c) transverse sections of the B horn core: (d) posterior view; (e) right lateral view; (f) medial view. The designation of epidermal scute areas (A, B, D and K) follows the system of Gaffney (1983).



Fig. 4. Partially restored posterior skull region of the Bullock Creek *Meiolania* compared with examples of *M. platyceps*. The *M. platyceps* examples, after Gaffney (1983; Fig. 22, AM F57984; Fig. 24, AM F1209; Fig. 38, AM F43183; Fig. 40, AM F61110), show the extremes of development in the B horn cores (AM F1209, largest; AM F43183, smallest) and the A horn cores (AM F57984, largest; AM F61110, smallest).

The dorsal, ventral, lateral and medial sides are flattened so that the transverse section at any point along the length resembles a rounded rectangle whose longest sides are aligned dorsoventrally. On the medial side there is a shallow, longitudinal suleus, restricted to the mid one-third of the length. The horn core surface is sculptured by nutrient foramina and canals.

The Bullock Creek B horn core is longer and more slender than any recorded example of *M. platyceps*. The ratio of the width at the base (estimated after restoration of the sheared-off portion) to the length, measured from the bone surface on the inside of the skull to the tip, is 0.32. This is outside the range (>0.40, <0.90) given for a sample of 50 *M. platyceps* B horn cores (Gaffney 1983).

2nd CERVICAL

5th CERVICAL

In proportions it more closely resembles the *M. mackayi* B horn core (Anderson 1925, Plate 32, Fig. 5).

M. platyceps has a pair of short, dorsoventrally-flattened A horn cores which project posterodorsally from the posterodorsal skull margin. This pair show a lesser degree of morphological variability than the B horn cores, and their size in any individual does not appear to be related to the degree of development of the B horn eore (Gaffncy 1983). On NTM P87103-2 the comparable region of the skull is slightly thickened in the posterior direction, but is not expanded into a foundation for a eranial horn (Fig. 4).

The Bullock Creek second cervical vertebra NTM P8695-93 (Fig. 5) is shorter anteroposteriorly, laterally compressed and dorsoventrally extended when compared with that of M. platyceps (Fig. 6). The lateral compression is reflected in the higher than wide central articulations and the shorter diapophyses (transverse processes). The neural spine is a broad, massive structure, rising high over the zygapophyses before arching anteroventrally and flaring laterally to an elevated position over the prezygapophyses. The ventral surface of the elevated part of the neural process has two, deep, oval fossae, separated by a medial keel, which may have provided for the deep insertion of rectus capitus muscles. In M. platyceps "the neural arch of the second cervical virtually lacks a neural spine, instead it is a broad, flat platform, that seems to articulate with the underside of the skull roof" (Gaffncy 1985:7). The neural process of the Bullock Creek cervical does have a flattened area, roughly diamond-shaped in dorsal view and somewhat smoother than the more rugose adjacent parts, which may represent that portion of the spine normally in articulation with the skull.

Other morphological features of the Bullock Creek second cervical conform with those of *M. platyceps*. The centrum is opisthococlous. Fused to the dorsoventral centrum margins were paired intercentra (Gaffney 1985), rcpresented only on the lcft side of NTM P8695-93 by the posterolaterally-projecting parapophysis. Its small, terminal, parapophyseal articular facet marks the point of attachment for the ventral head (capitulum) of the third cervical rib. The dorsal head (tuberculum) of the second cervical rib articulated over a relatively large surface at



Fig. 5. Bullock Creek *Meiolania* second cervical vertebra NTM P8695-93 and fifth cervical NTM P87103-4. Abbreviations: dia, diapophysis; ns, neural spine; para, parapophysis; prz, prczygapophysis; pz, postzygapophysis.

2nd CERVICAL

5th CERVICAL



Fig. 6. Bullock Creek *Meiolania* cervicals compared with examples of *M. platyceps*. AM F: 5547 and AM F:57984 after Gaffney (1985, Fig. 5), MM F: 13847 after Owen (1888, Plate 35, Figs 1-3).

the end of the robust diapophysis, which emerges partly from the neural arch and partly from the vertebra centrum. The cervical ribs of M. platyceps and their mode of attachment are described in detail by Gaffney (1985).

The prezygapophyses are borne on short anterior projections of the neural arch, emerging at about mid-level of the neural canal. Their articular facets are small and face dorsolaterally. The ventrolaterally-facing postzygapophyseal articular surfaces are relatively large and are situated high on the neural arch, entirely above the level of the neural canal. The Bullock Creek fifth cervical vertebra, NTM P87103-4, (Fig. 5) differs from *M. platyceps* in having a more upright neural spine and a kecled centrum (Fig. 6). The keel was intercepted by the rock drill during collection, but is complete enough for restoration. In *M. platyceps* the fifth cervical has indistinct, low, parasaggital ventral ridges (Gaffney 1985).

Proportionally, NTM P87103-4 falls within the range for M. platyceps, and apart from the features listed above, is morphologically similar. The centrum is procoelous; the anterior central articulation is deeply concave, and the posterior one, bulbous. The preserved left parapophysis is attached anterolaterally and has a small, posterolaterally-facing articular facct. The diapophyses, projecting laterally from midway along the centrum length at the contact of the neural arch and the centrum, have large, posterolaterally-facing articular surfaces. Both the prezygapophyses and postzygapophyses are widely separated and situated high on the neural arch. Their articular surfaces are relatively large and all are of a similar size. The prezygapophyseal articular surfaces face dorsomedially, while the postzygapophyseal articular surfaces face ventrolaterally. As in M. platyceps the neural spine is a low, blunt swelling.

DISCUSSION AND SYSTEMATIC DETERMINATION

Radiation within the Meiolaniidae is poorly understood with only M. platyceps well represented by fossil material. The cow-like B horn core and the absence of any osseous, posterodorsal cranial frill aligns the Bullock Creek horned turtle with Meiolania platyceps and M. mackayi and separates it from "Meiolania" oweni, Niolamia argentina and Crossochelys corniger. The Bullock Creek material is considerably older than the Pleistocene M. platyceps and M. mackayi but the geological range of meiolaniid taxa are as yet unknown. The general morphological similarity of the Bullock meiolaniid to M. platyceps justifies its assignment to the genus Meiolania, but a specific determination awaits the recovery of additional diagnostic material.

The distinctive features of the Bullock Creek meiolaniid, possibly of some taxonomic significance are, relative to *M. platyceps*: the long, slender, cow-like, B horn core projecting at a low angle; the absence of paired A horn cores; the short, laterally compressed, and dorsoventrally extended second cervical vertebra; and the keeled fifth cervical. The presence of some comparable features in other fragmentary material is intriguing.

Anderson (1925) distinguished M. mackayi from Walpole Island (New Caledonia) from M. platyceps by its smaller size and more slender cranial horn. The Bullock Creek cranial horn is relatively slender, and in this respect resembles M. mackayi. Anderson (1925) commented on the variability in the shape and size of the M. playtceps cow-like cranial horn and noted that a sufficiently large sample of M. mackayi might overlap with M. platyceps. M. mackayi remains poorly defined, the cervical vertebrae are unknown, and other postcranial elements differ from M. platyceps in size only.

Gaffney et al. (1984) describe two cervical vcrtebrae from New Caledonia. The Tiga Island centrum (NCT 01), probably of a seventh cervical, corresponds closely with M. platyceps examples from Lord Howe Island, but the complete Pindai Cave seventh cervical (NCP 05) retains a number of distinctive features. It differs from Lord Howe Island M. platyceps in having almost round (rather than laterally elongate) central articulations, a well-dcvcloped ventral ridge (keel) and no indication of broad sutural contact for the parapophyses. Gaffney et al. (1984) suggest that these three characters may be of some taxonomic significance, but were not able to assign the vertcbrae to any meiolaniid taxon. Unfortunately, no seventh cervical from Bullock Crcck has yet been recovered, but the laterally compressed second cervical with its higher than wide central articulations, and the keelcd fifth cervical, are suggestive, particularly if the sequential variation in the M. platyceps cervical series (Gaffney 1985) is used as a guide.

Also worthy of mention here is an unassociated, unusually short, atlantal neural arch from Lord Howe Island (AMF:18835) described by Gaffney (1985). Its degree of shortening relative to other examples from Lord Howe Island parallels the relative shortness of NTM P8695-93 compared with *M. platyceps* axis vertebrac. Gaffney (1985) commented that "..AM F18835 is not so easily interpreted as individual variation", but left it as an aberrant example of *M. platy-ceps*.

Etheridge (1989) described a ?Miocene (see Gaffney 1981:28; Woodburnc et al. 1985) meiolaniid from Gulgong, New South Wales. Gaffney (1981:29) regards it as "a taxon allied to Meiolania platyceps because of the 'cow-like' cranial horn but differing from the Lord Howe Island species in the low and thin shape of the horn" and noted that the lower jaw and tail club fragments also differed. The Gulgong B horn core is much smaller than the one from Bullock Creck, though this feature may be attributable to individual variation if *M. platyceps* is any guide. A cervical vertebra mentioned in a footnote by Etheridge (1889) has not been described.

Remains of a *M. platyceps*-sized meiolaniid have also bccn rccovcred from mid-Miocene (Woodburnc *et al.* 1985) sediments at Lakes Pinpa, Ngapakaldi and Pitikanta, South Australia. Manus clements are nearly identical to those of *M. platyceps* (Gaffney 1981:24). Apart from a plastron fragment, none of the material listed by Gaffney (1981) overlaps with Bullock Creek specimens currently avaliable.

The relationship of various forms apparently allied to M. platyceps cannot yet be convincingly demonstrated, but the possibilities bear brief mention. The distinctive features preserved with the fragmentary material listed above may simply represent temporal and geographic variants of an unbranching meiolaniid lincage culminating in M. platyceps. Thus, the Lord Howe Island M. platyceps could be derived directly from the Bullock Creek Meiolania by the development of A horn cores, loss or reduction of a ventral keel in the postcrior cervicals, and some changes in proportions. Alternatively, these character states may indicate a radiation, with some members of the genus Meiolania as sister taxa. One possibility has Meiolania platyceps and the Bullock Creek Meiolania sharing a common ancestor, with descendants of the Bullock Crcek form persisting into the Pleistocene or Recent of New Caledonia. An alternative theory of radiation involves a split in post Bullock Creek times, with the appearance of derived features in the M. platyceps lineage, and retention of a more plesiomorphic character complex in a New Caledonian form.

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